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Author(s): Deborah Wall-Palmer, Christopher W. Smart, Malcolm B. Hart, Melanie J. Leng, Mireno Borghini, Elena Manini, Stefano Aliani and Alessandra Conversi

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Micropaleontology

Late Pleistocene pteropods, heteropods and planktonic foraminifera from the Caribbean Sea, Mediterranean Sea and Indian Ocean

Deborah Wall-Palmer^{1,2}, Christopher W. Smart^{1,2}, Malcolm B. Hart^{1,2}, Melanie J. Leng³, Mireno Borghini⁴, Elena Manini⁵, Stefano Aliani⁴ and Alessandra Conversi^{2,4}

¹School of Geography, Earth and Environmental Sciences, Plymouth University, Plymouth, PL4 8AA, UK

²Marine Institute, Plymouth University, Plymouth, PL4 8AA, UK

³Department of Geology, University of Leicester, Leicester, LE1 7RH, UK & NERC Isotope Geosciences Laboratory, British Geological Survey, Keyworth, Nottingham, NG12 5GG, UK

⁴ISMAR-CNR, Forte Santa Teresa, Pozzuolo di Lerici, 19036 La Spezia, Italy

⁵ISMAR-CNR, Largo Fiera della Pesca, 60125 Ancona, Italy

email: deborah.wall-palmer@plymouth.ac.uk

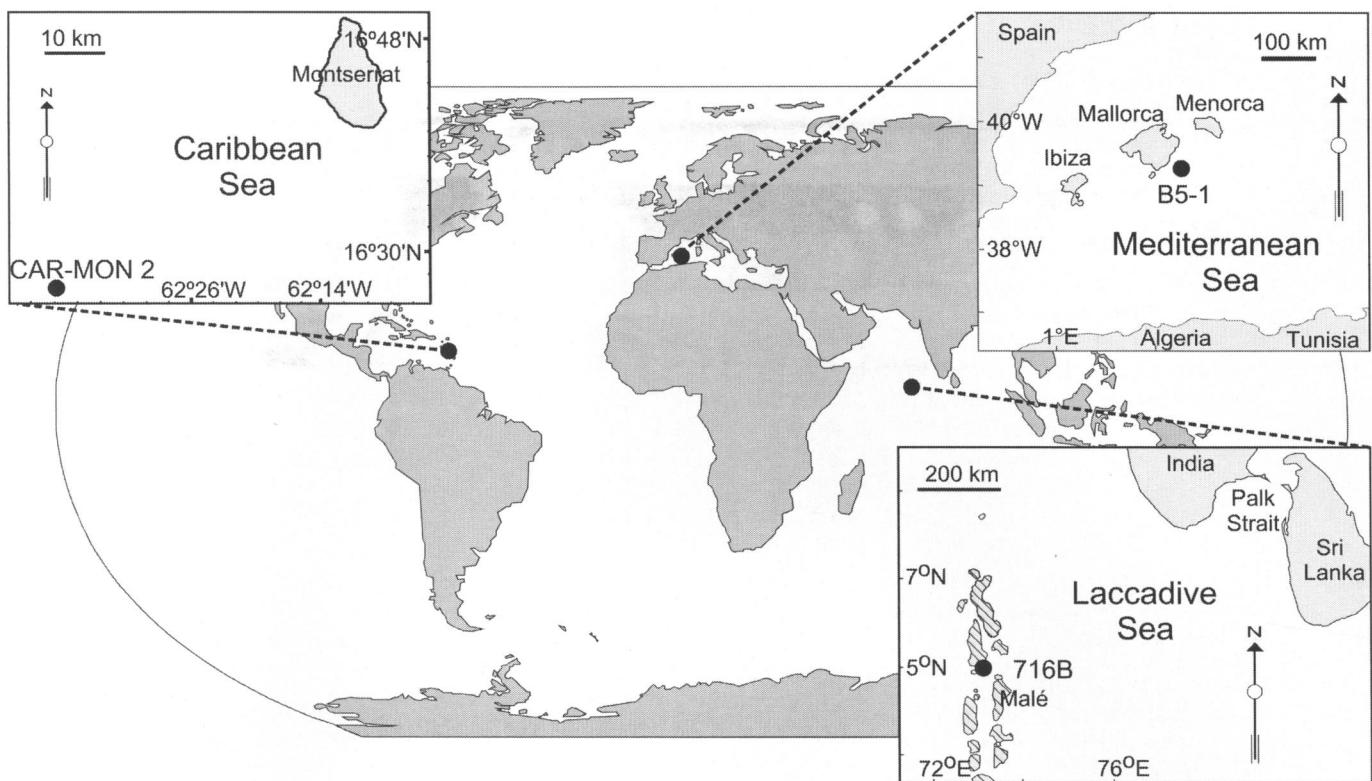
ABSTRACT: Pteropods and heteropods (holoplanktonic gastropods) are an important component of the modern oceans; however, detailed information on their distribution in the fossil record is often based on poorly preserved specimens. This study presents the micropaleontological analysis of three exceptionally well-preserved Late Pleistocene marine sediment cores from the eastern Caribbean Sea, western Mediterranean Sea and the Indian Ocean. This study presents the first stratigraphical record of heteropods in the Caribbean Sea and extends the known zonation of pteropods in the Mediterranean Sea. Distributions of pteropods, heteropods and planktonic foraminifera are presented with abundance and species richness data, as well as stratigraphical dates inferred from the oxygen isotope stratigraphy, argon-argon dating and biostratigraphy. The findings of this study greatly improve our understanding of holoplanktonic gastropod stratigraphy and ecology. Results reveal that the geographical range of heteropods, thought to be restricted to sub-tropical warm waters, may be much greater, including waters of sub-polar temperature. Heteropods were also found to be surprisingly abundant, potentially representing a more important part of the ocean food web than previously thought. Analysis revealed two species of holoplanktonic gastropod that are previously undescribed and indicate that the pteropod *Heliconoides mermuysi* (Cahuzac and Janssen 2010), known exclusively from the Moulin de Cabanes (Miocene), may have lived in the Caribbean Sea and Indian Ocean as recently as 4 kyr ago. These findings highlight the urgent need for increased research on holoplanktonic gastropods. The threat that current climate change and ocean acidification poses, particularly to the delicately shelled forms, means that some species may become extinct before they have even been fully 'discovered'.

INTRODUCTION

Pteropods and heteropods are planktonic gastropods, which have evolved wings from the foot structure that characterises animals in the class Gastropoda. These wings are uniquely adapted to enable the animals to live their entire lives as a planktonic form (Bé and Gilmer 1977) and they are, therefore, termed holoplanktonic. Pteropods are a common component of the water column throughout the world's oceans (Bé and Gilmer 1977) and consist of two orders; the shell-less gymnosomes and the shell-bearing thecosomes. These two orders are now considered to be less closely related than originally thought (Lalli and Gilmer 1989) despite superficial similarities, although, the term pteropod is still widely used. This study focuses on the order Thecosomata, which is made up of shelled species in the suborders Euthecosomata and Pseudothecosomata. The Heteropoda, more recently known as the superfamily Pterotracheoidea, are less well-known. They consist of three families: one shelled, the Atlantidae, one with reduced shells, the Carinariidae, and one shell-less, the Pterotracheidae. Representatives of all three families, including larval shells of the Pterotracheidae, were found during this study. At present, the distribution and abundances of heteropods are not known in detail. Available information sug-

gests that they are found in moderate to low abundances primarily in tropical and sub-tropical warm water regions (Thiriot-Quiévreux 1973; Lalli and Gilmer 1989; Seapy 2011). However, the results of this study indicate that heteropods can also reside in sub-polar waters, since they were found to be abundant in sediments from glacial periods in the geological past.

Shells produced by pteropods and heteropods are formed of aragonite, a polymorph of calcium carbonate, which is particularly susceptible to dissolution (50% more susceptible than calcite). Consequently, in over 98% of the oceans, all of the aragonite shells produced are dissolved while sinking through the water column or during early sedimentation (Byrne et al. 1984; Fabry 1990). The fossil record of pteropod and heteropod shells is, therefore, restricted to sediments in shallow water that is supersaturated with respect to aragonite. The known stratigraphical range of pteropod shells extends from the Recent to the Paleogene (Lokho and Kumar 2008; Janssen and Peijnenburg 2013), with the first known occurrence in the latest Paleocene of Europe (Janssen and King 1988) and North America (Janssen et al. 2007). The fossil record of heteropods is less well-known, however, the stratigraphical range is known to extend from the Recent to the Jurassic (Janssen and Peijnenburg 2013).



TEXT-FIGURE 1

Location of core sites: CAR-MON 2 south-west of Montserrat in the Lesser Antilles island arc, eastern Caribbean Sea; B5-1 south-east of Mallorca in the western Mediterranean Sea; ODP Site 716, Hole B on the Chagos-Laccadive Ridge, amongst the Maldives Islands in the Indian Ocean.

Holoplanktonic gastropod shells are rarely used in biostratigraphy because of their susceptibility to dissolution. However, the sensitivity of living holoplanktonic gastropods to changes in environmental conditions makes them extremely valuable both for stratigraphical correlation and paleoenvironmental reconstructions. This study aims to improve the use of holoplanktonic gastropods in biostratigraphy by documenting their stratigraphical distributions throughout three Late Pleistocene sediment cores from the Caribbean Sea, the Mediterranean Sea and the Indian Ocean. In particular, the results of this study extend the known zonation of pteropods in the Mediterranean Sea, both spatially and stratigraphically, allowing a detailed paleoenvironmental reconstruction. Results also contribute to a greater understanding of holoplanktonic gastropod ecology and taxonomy.

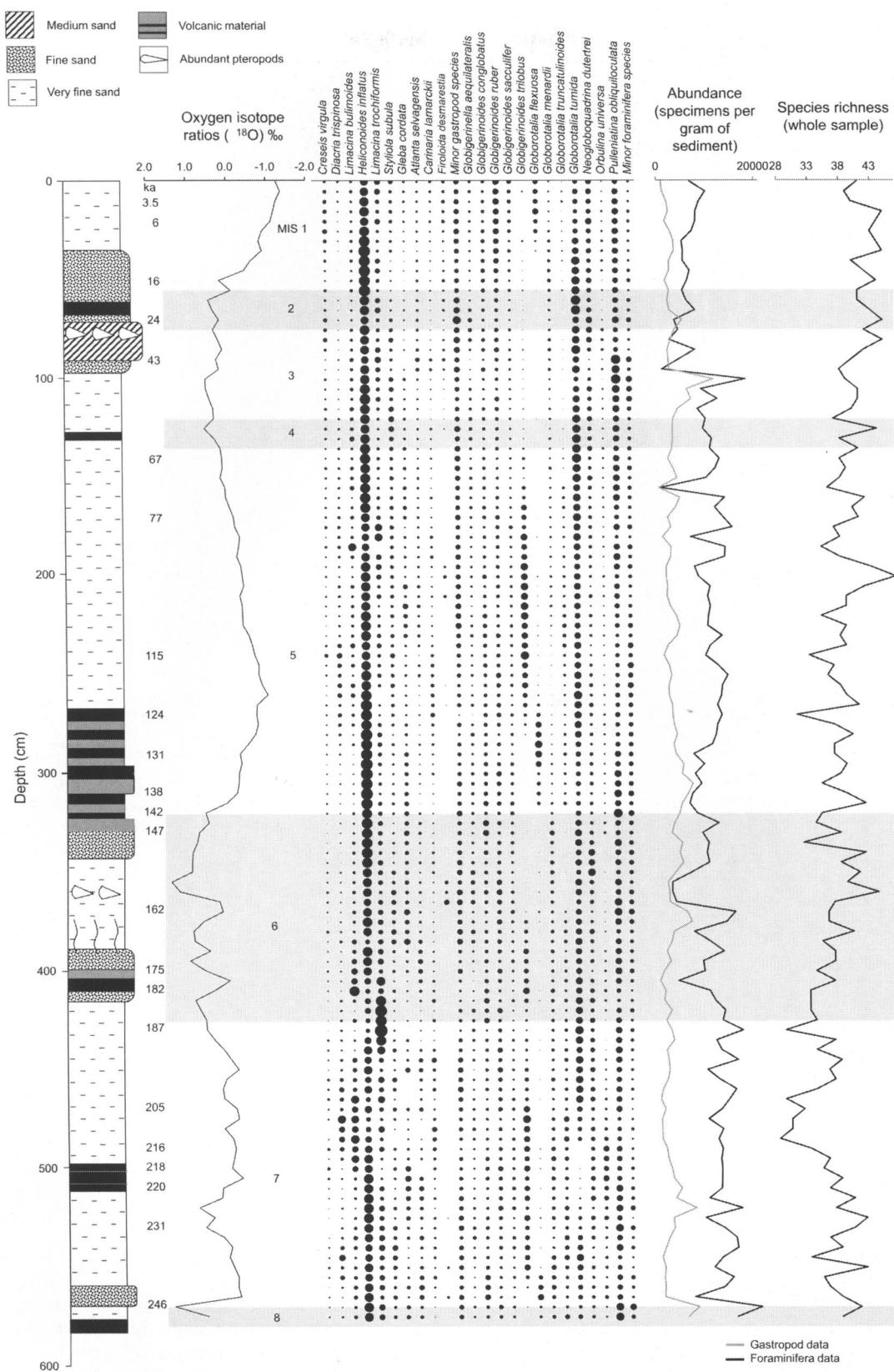
METHODOLOGY

Sampling sites

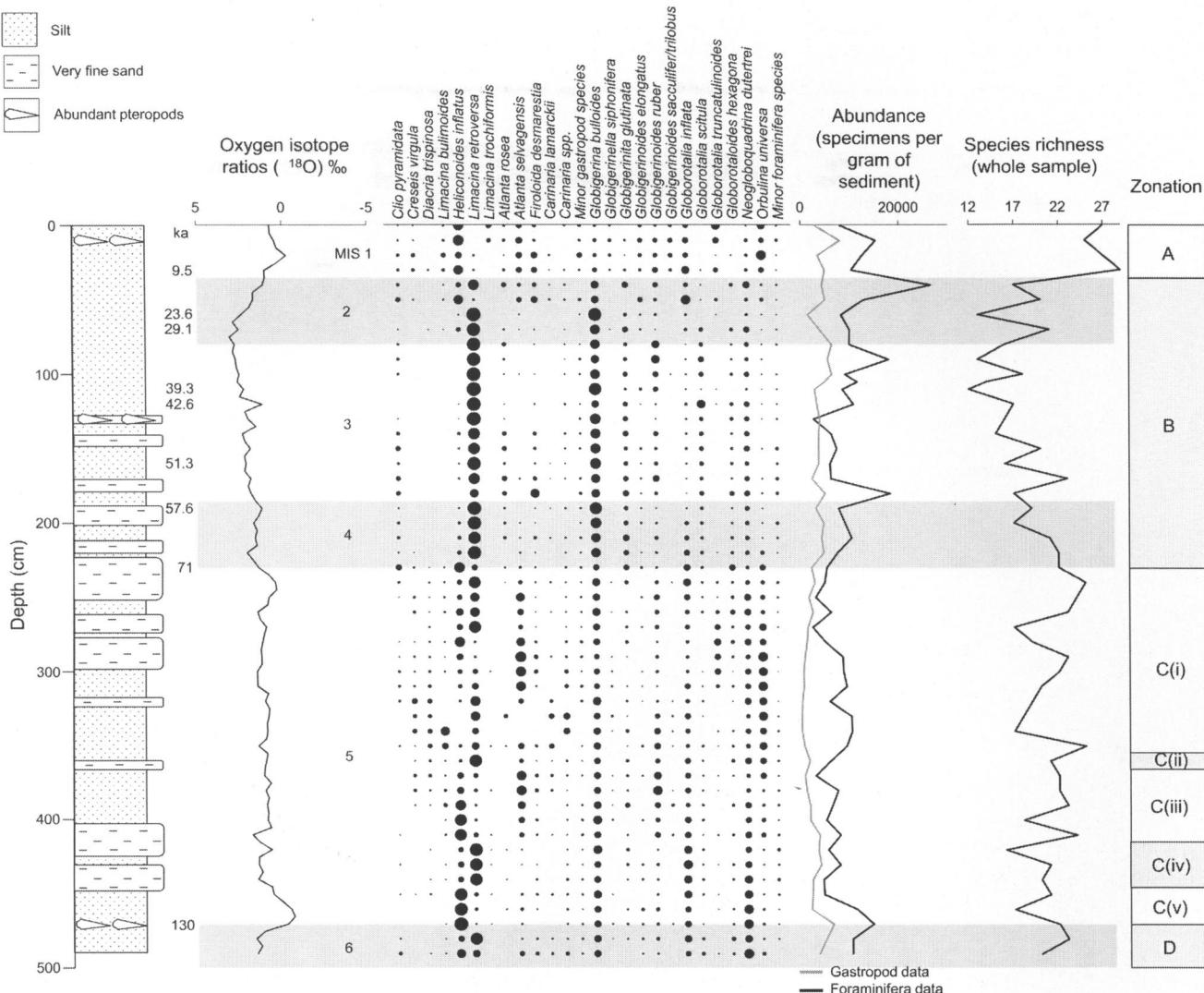
For this study, three core sites situated well above the Aragonite Lysocline (ALy) were chosen to reduce the effects of post-depositional dissolution (Gerhardt and Henrich 2001; Sabine et al. 2002; Schneider et al. 2007). All three cores show exceptional preservation, indicated by surface sediment assemblages of planktonic foraminifera and holoplanktonic gastropods, which are comparable to those in the overlying waters. This implies that specimens have not been affected by dissolution or transportation, retaining an accurate representation of the abundance and species richness of the overlying waters.

Low fragmentation of planktonic foraminifera tests and extremely well preserved pteropod shells also indicate little to no post-depositional dissolution.

Core CAR-MON 2 was collected to the south-west of Montserrat ($16^{\circ}27.699'N$, $62^{\circ}38.077'W$, water depth 1102 m) in the Lesser Antilles volcanic arc (text-fig. 1) and was sampled at 5cm (~2.2 kyr) intervals. Oxygen isotope stratigraphy (text-fig. 2) and additional data for CAR-MON 2 has previously been published by Le Friant et al. (2008), Messenger et al. (2010) and Wall-Palmer et al. (2012, 2013). Core B5-1 was collected to the south-east of the Balearic island of Mallorca ($39^{\circ}14.942'N$, $03^{\circ}25.052'E$, water depth 1519m) in the western Mediterranean Sea (text-fig. 1). B5-1 was sampled for microfossil analysis at 10cm (~2.7 kyr) intervals and oxygen isotope stratigraphy at 5cm intervals (text-fig. 3). The stratigraphy of B5-1, based on oxygen isotope stratigraphy and biozonation of planktonic foraminifera (text-fig. 4), is reported in this study. Indian Ocean Hole 716B was collected by the Ocean Drilling Program, from a shallow site (Site 716, $04^{\circ}56.0'N$, $73^{\circ}17.0'E$, water depth 533m) on the Chagos- Laccadive Ridge within the Maldives Islands (text-fig. 1). Of the cores collected at Site 716, this study is based on the upper 13m of Hole B, which was recognised by Droxler et al. (1990) to contain abundant holoplanktonic gastropods. Oxygen isotope stratigraphy (text-fig. 5) for Hole 716B has been previously published by Backman et al. (1988) and Droxler et al. (1990). Hole 716B was sampled at a low resolution at points corresponding to major changes in climate, which were identified with the use of oxygen isotope stratigraphy (Backman et al. 1988).



TEXT-FIGURE 2
CAR-MON 2 Lithology, Oxygen isotope ratios and Marine Isotope Stages, species assemblages, abundances by weight and species richness. Bubble areas represent percentages, calculated separately for gastropods and planktonic foraminifera. Dates from Le Friant et al. (2008).



TEXT-FIGURE 3

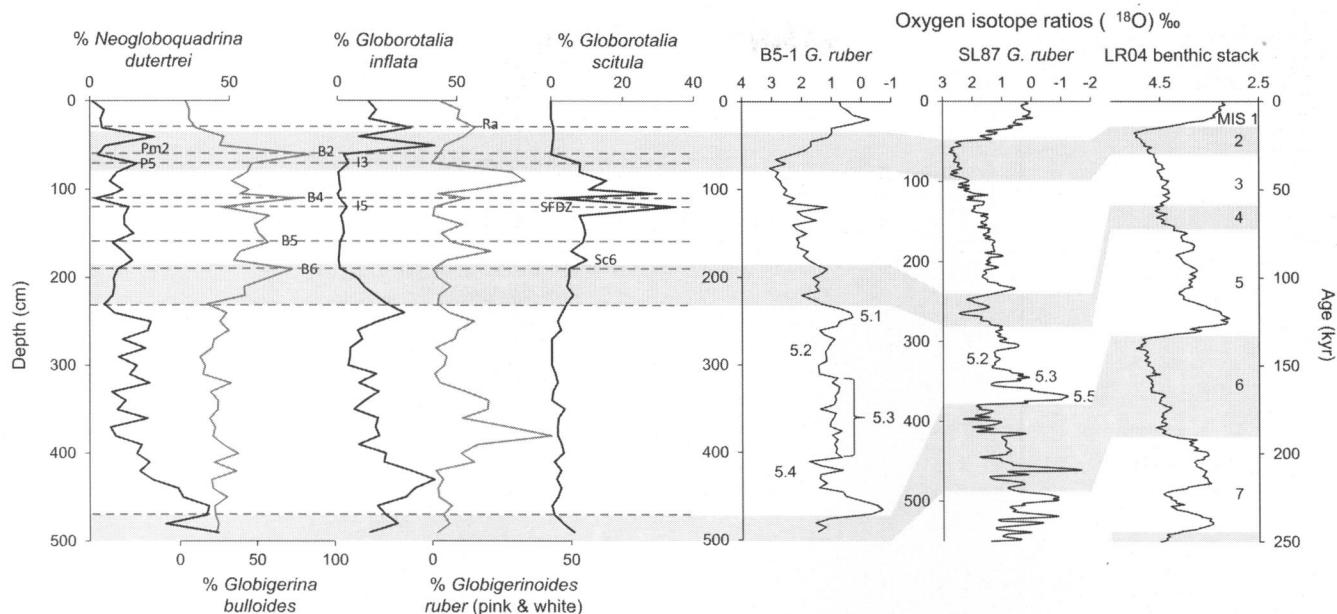
B5-1 Lithology, Oxygen isotope ratios and Marine Isotope Stages, species assemblages, abundances by weight and species richness. Bubble areas represent percentages, calculated separately for gastropods and planktonic foraminifera. Dates from biozonation and isotope stratigraphy.

Microfossil analysis

No chemicals were used during sample processing. Dried samples were gently disaggregated, weighed and re-hydrated using deionised water (pH 7.89). Each sample was then washed over a 63 µm sieve, filtered and air dried. Dried samples were then weighed to calculate the amount of <63 µm sediment that had been removed during washing. Counts of planktonic foraminifera and holoplanktonic gastropods were made from two size fractions, 150–500 µm and >500 µm, in order to provide representatives of both small and large species. Results from the two fractions have been combined for all subsequent data analysis. For each sample, just over 300 (or until the sample was exhausted) planktonic foraminifera and just over 300 (or until the sample was exhausted) holoplanktonic gastropod specimens were counted and identified from both size fractions. Only whole specimens and fragments retaining the proloculus or

protoconch were counted to avoid the distortion produced by several fragments of the same specimen. Samples were weighed before and after analysis to calculate the overall abundance of microfossils (specimens per gram of sediment).

The identification of planktonic foraminifera was made using the taxonomic reviews by Bé (1977), Saito et al. (1981) and Kennett and Srinivasan (1983). The identification of pteropod species was made using the keys published by Bé and Gilmer (1977), Van der Spoel (1976) and Janssen (2012), with additional information from Tesch (1946, 1949). Identification of heteropods was made using Tesch (1949), Thiriot-Quiévreux (1973), Seapy (1990), Janssen (2012) and the online guide compiled by Seapy (2011). Counts of microfossils are expressed as a percentage (relative abundance) of the total number of specimens, separately for planktonic foraminifera and holoplanktonic gastropods.



TEXT-FIGURE 4

Stratigraphy of B5-1 with bio-events of Pujol and Vergnaud-Grazzini (1989) and Pérez-Folgado et al. (2003) identified within B5-1 planktonic foraminifera data. Oxygen isotope stratigraphy of B5-1 and comparison of the marine oxygen isotope records for B5-1, SL 87 (Weldeab et al., 2003), approximately 60 km south east of B5-1, and the LR04 benthic stack (Lisiecki and Raymo, 2005).

Stable isotope analysis and stratigraphical framework for B5-1

Stable isotope analysis of core B5-1 were carried out at the Natural Environment Research Council (NERC) Isotope Geosciences Laboratory, British Geological Survey, Keyworth. Ten specimens of *Globigerinoides ruber* (d'Orbigny 1839) of size 250 μ m to 355 μ m were analysed from each sample at 5cm intervals, using a GV IsoPrime mass spectrometer plus Multiprep device. Isotope values ($\delta^{18}\text{O}$) are reported as per mille (‰) deviations of the isotopic ratios ($\delta^{18}\text{O}/^{16}\text{O}$) calculated to the VPDB scale using a within-run laboratory standard calibrated against NBS standards (^{13}C were analysed but are not reported here). Analytical reproducibility of the standard calcite (KCM) is <0.1‰ for $\delta^{18}\text{O}$. The isotope profile produced is comparable to published data for sediments in the area (Weldeab et al. 2003). Marine $\delta^{18}\text{O}$ data are used as a proxy for global ice volume and data can, therefore, be compared globally. By comparing the $\delta^{18}\text{O}$ record within core B5-1 to a globally standardised record, such as the LR04 stack (Lisiecki and Raymo 2005), glacial and interglacial periods, termed Marine Isotope Stages (MIS), can be identified, dating certain parts of the core. The $\delta^{18}\text{O}$ data show that B5-1 contains a marine isotope record extending back to MIS 6. Alignment of the MIS (text-fig. 4) was achieved by comparison to the $\delta^{18}\text{O}$ record published by Weldeab et al. (2003) for site SL87 (text-fig. 4), approximately 60km south east of B5-1 and the LR04 stack (Lisiecki and Raymo 2005).

Planktonic foraminifera distributions within B5-1 were also used to date parts of the core and refine the position of MIS boundaries. The down-core distributions of several key species reflect the bio-events identified by Pujol and Vergnaud-Grazzini (1989) and Pérez-Folgado et al. (2003) in the Mediter-

ranean Sea (text-fig. 4). These events indicate several minor climatic episodes, providing additional dating points throughout the upper 190cm of the core.

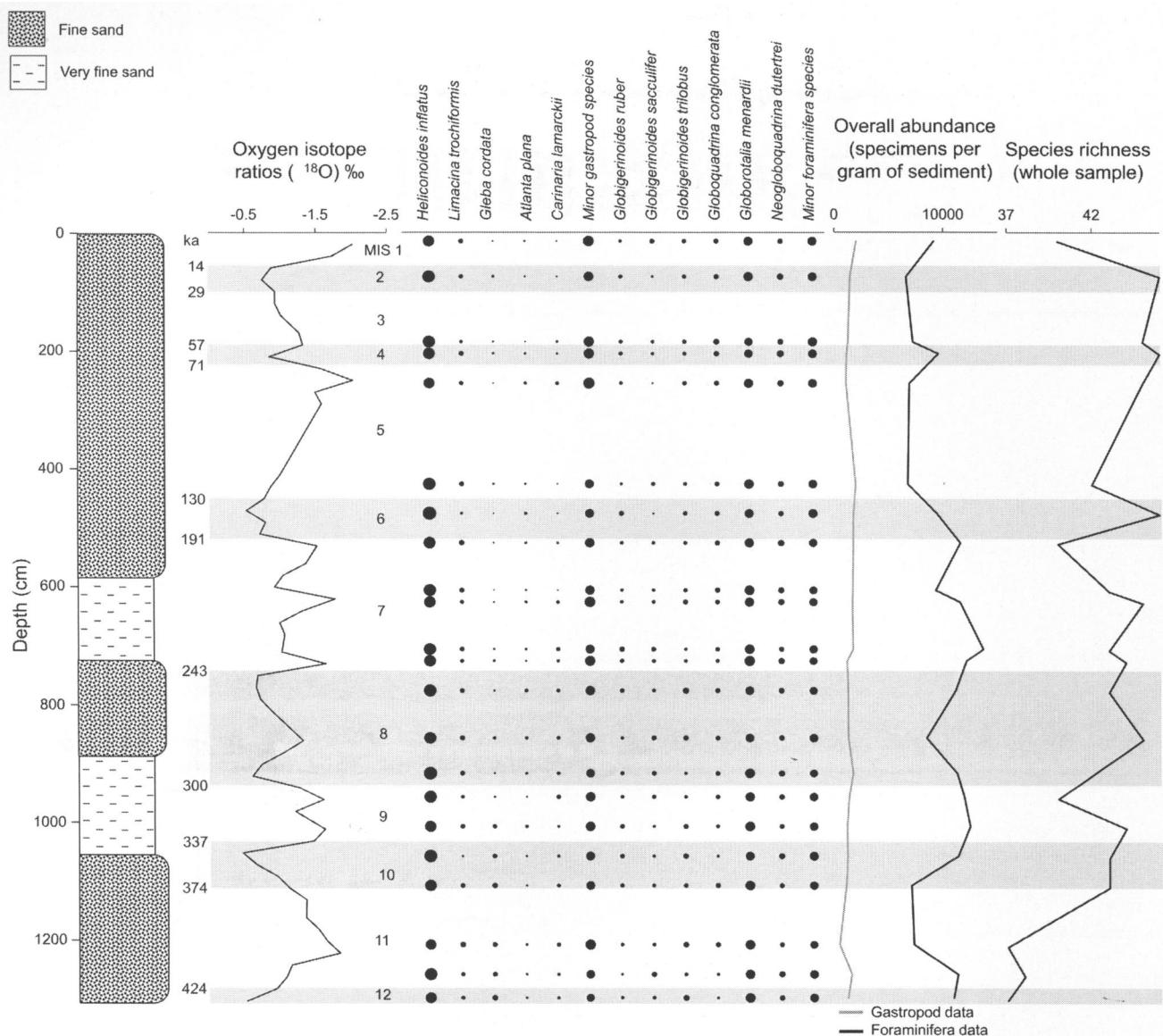
Statistical analysis

Cluster analysis was carried out for Mediterranean Sea core B5-1, where changes in species composition appear to be strongly influenced by changes in climate. Cluster analysis has been used in this study to identify whether apparent warm and cold water assemblages are significantly different from one another. Cluster analysis was carried out using the Paleontological Statistics package (PAST). The Paired-Group algorithm and Euclidian similarity measure were used.

RESULTS

The Caribbean Sea

The assemblage of planktonic foraminifera and holoplanktonic gastropods in the surface sediments of CAR-MON 2 is comparable to that of the overlying waters and this sedimentary record is, therefore, useful in reconstructing the paleoenvironmental conditions at this site. The similarity between surface sediment microfossil content and living assemblages in the Caribbean Sea has previously been demonstrated by Wells (1975), who found that euthecosome pteropods deposited in the surface sediments close to Barbados accurately reflect the species composition and relative abundances of the overlying waters. All species of pteropod found in the surface waters of the Western Caribbean Sea (Wells 1975, 1976; Parra-Flores 2009) are present in CAR-MON 2 sediments. The majority are represented within the surface 1cm of sediment. The distribution of living shelled heteropods is not well documented and no published data from the Caribbean Sea were found. It is assumed that, like the



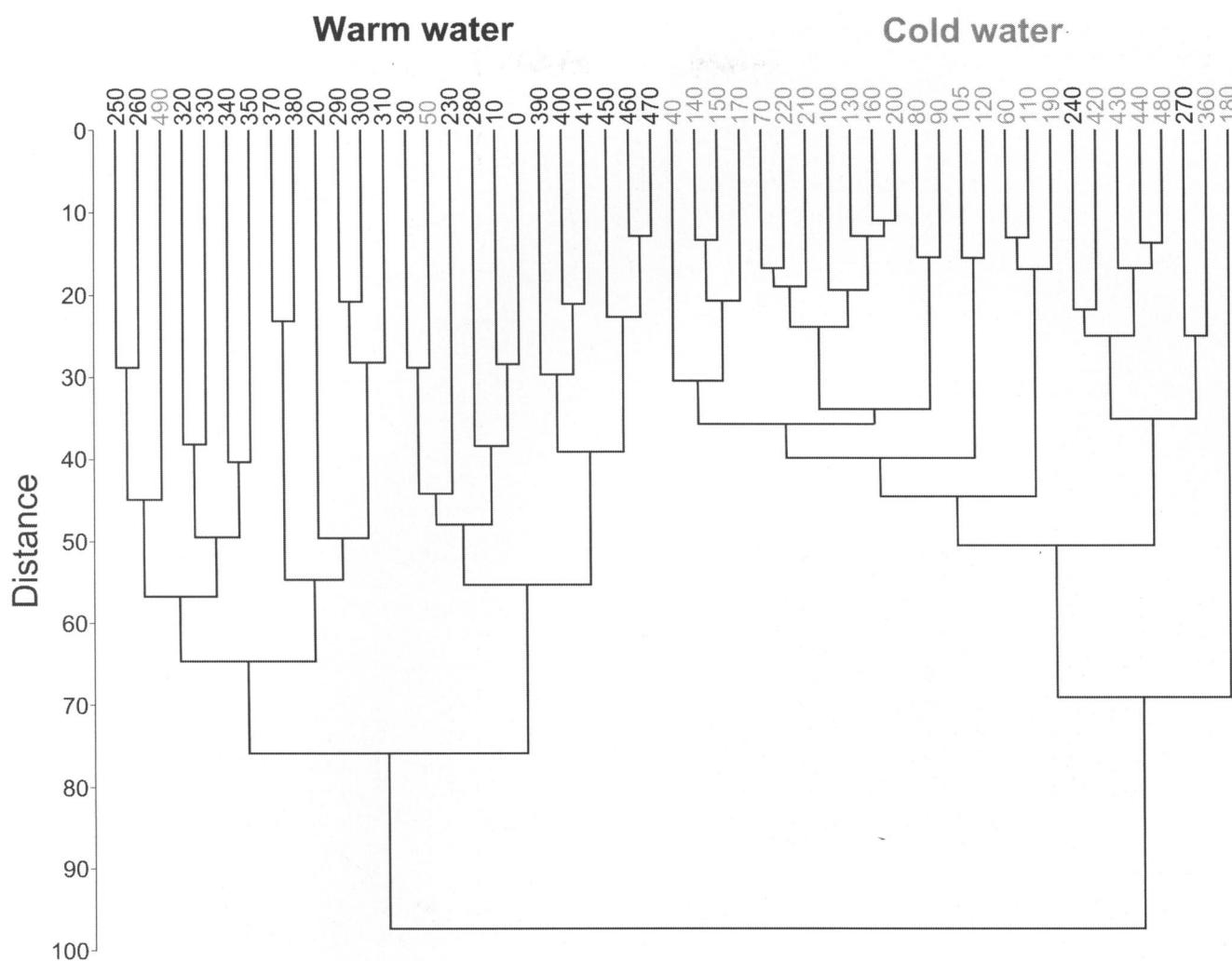
TEXT-FIGURE 5

Hole 716B Lithology, Oxygen isotope ratios and Marine Isotope Stages, species assemblages, abundances by weight and species richness. Bubble areas represent percentages, calculated separately for gastropods and planktonic foraminifera. Dates from isotope stratigraphy (Backman et al. 1988).

shelled pteropods, the living assemblage of heteropods is well represented within the surface sediments of CAR-MON 2. No extensive studies have been made of the modern living planktonic foraminifera assemblage of the Caribbean Sea. More generally, Bé and Tolderlund (1971) described the distribution of living planktonic foraminifera in the surface waters of the Atlantic. This study includes species distribution maps, which allow the living planktonic foraminifera assemblage of the Lesser Antilles to be inferred. All species included in the maps of Bé and Tolderlund (1971) for the Lesser Antilles are present within the surface sediments of CAR-MON 2 with one exception, *Hastigerina pelagica* (d'Orbigny 1839), which is absent from the entire core. However, Bé and Tolderlund (1971) only found *H. pelagica* to be present within the surface waters in low numbers (0.1–4.9 %) and it may, therefore not have been present in

the waters overlying this site. Although there appear to be several species present within the surface sediments of CAR-MON 2 that were not found by Bé and Tolderlund (1971), these are mainly recently described species. For example, *Globigerinoides trilobus* (Reuss 1850) would have been included within the counts of *Globigerinoides sacculifer* (Brady 1877) by Bé and Tolderlund (1971), but has now been identified as a separate species.

Due to the low latitude location of the Caribbean Sea, and the consequent low variation in surface water temperature across glacial and interglacial periods, CAR-MON 2 shows that very little change in species composition and species richness (28–47 species) occurred over the last 250 kyr (text-fig. 2). The lack of significant synchronous changes between oxygen isotope data



TEXT-FIGURE 6

Cluster analysis of B5-1 samples performed using the Paleontological Statistics package (PAST). Abundances of pteropods, heteropods and planktonic foraminifera show two defined groups with similar assemblages, preferring either warm or cold water.

and the relative abundances of temperature sensitive species (text-fig. 2) supports this observation. The overall abundance (specimens per gram of sediment) of holoplanktonic gastropods and planktonic foraminifera shows greater variation, but does not change synchronously with oxygen isotope data, suggesting that factors such as nutrient availability have produced the fluctuations in overall abundance. Foster (2008) reconstructs the range in temperature from the last glacial maximum at MIS 2.2 to the last interglacial maximum at MIS 5.5 as being between 25.7 and 29.1°C. Schmidt et al. (2006) show a comparable reconstruction for Caribbean surface water, finding temperatures between 2.1–2.7°C colder than the present during the last three glacial maxima. The species assemblage throughout CAR-MON 2 is composed of warm water sub-tropical species of planktonic foraminifera and holoplanktonic gastropods. Dominant planktonic foraminifera species include *G. ruber*, *G. sacculifer* (including *G. trilobus*) and *Neogloboquadrina dutertrei* (d'Orbigny 1839). Other common species include *Globigerinella siphonifera* (d'Orbigny 1839), *Globigerinoides conglobatus* (Brady 1879), *Globigerinita glutinata* (Egger 1893) and *Globorotalia truncatulinoides* (d'Orbigny 1839).

The pteropod genera *Limacina* and *Heliconoides* dominate the assemblage of holoplanktonic gastropods. The most abundant species is *Heliconoides inflatus* (d'Orbigny 1834), which comprises up to 68% of the holoplanktonic gastropod population. Other common and often abundant species of pteropod include *Creseis clava* (Rang 1828), *Creseis virgula* (Rang 1828), *Limacina bulimoides* (d'Orbigny 1834), *Limacina trochiformis* (d'Orbigny 1834) and *Stylola subula* (Quoy and Gaimard 1827). The dominant heteropod genus is *Atlanta*, with the most abundant species being *Atlanta peronii* Lesueur 1817 and *Atlanta selvagensis* de Vera and Seapy 2006. Other common and often abundant heteropod species include *Firoloidea desmarestia* Lesueur 1817 and *Carinaria lamarckii* Blainville 1817.

The Mediterranean Sea

The surface sediments of B5-1 contain a comparable assemblage of planktonic foraminifera and holoplanktonic gastropods to that of the overlying waters. In agreement with the distribution of living pteropods in the western Mediterranean Sea (Bé and Gilmer 1977), the surface sediments of B5-1 contain a single extremely abundant pteropod species (*H. inflatus*), with

many more present in low numbers. Limited data on modern Mediterranean heteropod species (Richter 1968; Thiriot-Quiévreux 1973) indicate that the surface sediments of B5-1 contain six out of the seven species which live in the overlying waters. There are also some species that were found within the surface sediments of B5-1 that are not recognised from the Mediterranean Sea. These include *Atlanta rosea* Gray 1850 and *A. selvagensis*, which are found in tropical and sub-tropical waters of the Atlantic and Indian oceans. This is partly due to the improved recognition of species, since *A. selvagensis* was not described until 2006 (de Vera and Seapy 2006) and specimens previously identified as *Atlanta inflata* Gray 1850 are now thought to belong to the species *A. selvagensis* in the Atlantic Ocean. Planktonic foraminifera within the surface sediments of B5-1 are also representative of the assemblages found in overlying waters (Bé 1977; Pujol and Verhaud-Grazzini 1995; Parker 2002). However, several of the species (including *Globorotalia hirsuta* (d'Orbigny 1839), *Globigerina falconensis* Blow 1959, *H. pelagica* and *G. glutinata*) which Bé (1977) described as being dominant, are not found in the surface sediments of B5-1. All but one species of planktonic foraminifera, *G. siphonifera*, found within the surface sediments of B5-1 are recorded from the Mediterranean Sea. This suggests that the sediments at this site have not been affected by post-depositional dissolution, allowing the microfossil assemblage to be used in reconstructing paleoenvironmental conditions.

Climatic events within the Mediterranean Sea tend to be amplified due to the semi-enclosed nature of the basin (Pérez-Folgado et al. 2003). Considerable variations in species composition therefore occur across glacial and interglacial periods. These variations have been used by several authors to reconstruct the past climate of the central and eastern Mediterranean Sea (Chen 1968; Herman 1971; Jorissen et al. 1993; Capotondi et al. 1999; Sbaffi et al. 2001; Janssen 2012), the Tyrrhenian Sea (Carboni and Esu 1987; Biekart 1989; Asioli et al. 1999; Buccheri et al. 2002), the Adriatic Sea (Jorissen et al. 1993; Asioli et al. 1999) and more generally the entire Mediterranean Sea (Hayes et al. 2005).

Throughout B5-1, species richness changes synchronously with the oxygen isotope data (text-fig. 3), suggesting a strong link to water temperature. Core B5-1 contains two distinct planktonic assemblages, which divide the core into four major zones (Zone C is further subdivided into five sub-zones), two of which (Zones B and A) have been previously recognised (Herman 1971; Carboni and Esu 1987; Jorissen et al. 1993; Capotondi et al. 1999; Sbaffi et al. 2001; Buccheri et al. 2002). These zones coincide with the MIS and are characterised by a homogenous set of species preferring either sub-polar cold water or sub-tropical warm water (text-fig. 3). The distinct assemblages can be identified using cluster analysis (text-fig. 6) which shows that the holoplanktonic gastropod and planktonic foraminifera assemblage of samples present within cold water Zones D, C(iv), C(ii) and B is approximately 97% different to the assemblage of samples within warm water Zones C(v), C(iii), C(i) and A. There are four samples, 50, 240, 270 and 490cm, which appear to be present in the incorrect cluster. However, these samples all contain a slightly different assemblage from other samples within their zone. For example, samples 50 and 490 show a sudden reduction in cold water species and an increase in warm water species, representing a very short warm fluctuation in the

otherwise cold Zone B. Therefore, instead of occurring in the cold water cluster, they are placed in the warm water cluster.

Zone D (490–476cm) ~133–130 ka

Zone D occurs within MIS 6 and is a known cool period, with a high global ice volume. The species present during this period are representative of a sub-polar assemblage similar to that of the modern North Atlantic (Bé and Gilmer 1977; Bé 1977). It is very similar in composition to Zone B (text-fig. 3), with high numbers (25–73% of holoplanktonic gastropods) of the sub-polar pteropod species *Limacina retroversa* (Fleming 1823) and low numbers of *H. inflatus* (18–38%). Cluster analysis shows that, at 490cm, there is a fluctuation in the dominant species of pteropod (text-figs 4 and 5), indicating a comparable composition to warmer zones. The presence of some warm water transitional species also suggests that this is the late transition from a colder period, which was not recovered in the core. The dominant species of planktonic foraminifera and pteropods during this period suggest an annual sea surface temperature range of 12–16°C (Bé and Tolderlund 1971; Bé and Gilmer 1977).

Zone C (475–226cm) 130–71 ka

This is a zone mainly composed of warm sub-tropical to tropical planktonic species. It spans the whole of MIS 5 and contains alternating warm periods with short term cooler periods. It signifies a gradual warming from the boundary of MIS 6 throughout MIS 5. The overall species composition of Zone C is similar to that of the modern western Mediterranean Sea (text-fig. 3).

Sub-Zone C (v) (475–446cm)

This is a short warm period, occurring during MIS 5.5, characterised by an increase in the abundance of *H. inflatus* (77–94%) and a coinciding decrease in the abundance of *L. retroversa* (1–8%). It is similar in species composition to Zone C(i) and C(iii). Cold water species do not disappear, but remain in lower numbers. Dominant planktonic foraminifera and pteropod species during this period suggest an annual sea surface temperature range of 16–19°C (Bé and Tolderlund 1971; Bé and Gilmer 1977). However, since MIS 5.5 was the last interglacial maximum and shows the greatest oxygen isotope excursion, dominant fauna should indicate the highest temperature within the core. Bardaji et al. (2009) estimate mean annual sea surface temperature at MIS 5.5 to be 23–24°C and never below 19–21°C during the winter.

Sub-zone C (iv) (445–416cm)

This is a short cooler period, occurring during MIS 5.4 and is characterised by a sharp peak in *L. retroversa* (from 8% at 450cm to 85% at 420cm) and a coinciding reduction in the abundance of *H. inflatus* (from 77% at 450cm to 12% at 420cm). The warm water species, such as *L. bulimoides* and *A. selvagensis*, do not disappear, but remain at a lower abundance, suggesting that this period is cooler but not sub-polar. *Globigerina bulloides* d'Orbigny 1826, a dominant species of planktonic foraminifera in sub-polar provinces (Bé 1977), is also present, but in low numbers. Dominant planktonic foraminifera and pteropod species during this period suggest an annual sea surface temperature range of 12–16°C (Bé and Tolderlund 1971; Bé and Gilmer 1977).

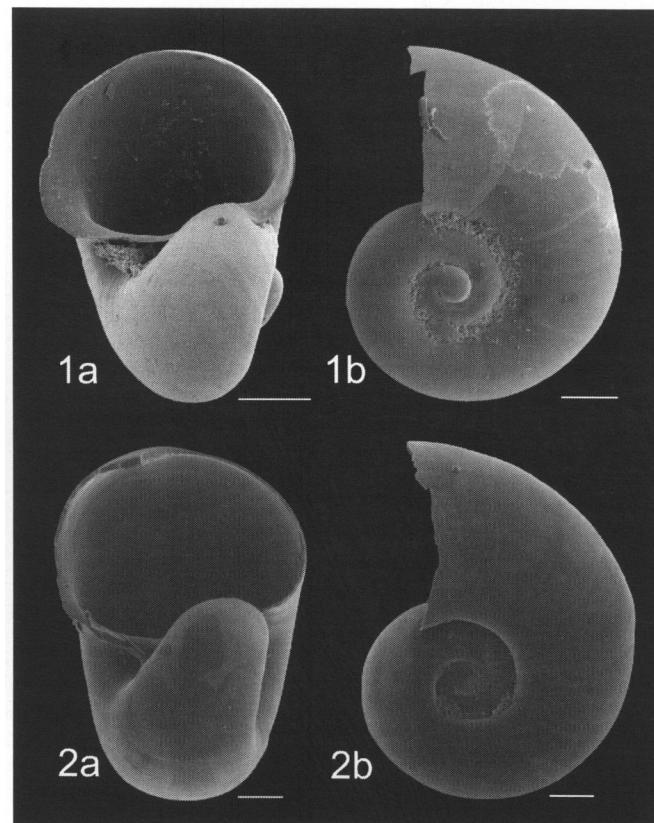
Sub-zones C (iii) 415–366cm; ii) 365–356cm; i) 355–226cm

This section is characterised by a relatively high abundance (up to 44% of planktonic foraminifera) of the sub-tropical planktonic foraminifera *Orbulina universa* d'Orbigny 1839. In common with Zone A, it contains a higher abundance of the pteropod *H. inflatus* (average 24%), the heteropod *A. selvagensis* (average 24%) and the planktonic foraminifera *Globorotalia inflata* (d'Orbigny 1839, 8–28%) and a generally low abundance of the sub-polar pteropod *L. retroversa* (variable between 2–72%). During Sub-Zone C (iii), dominant planktonic foraminifera and pteropod species suggest an annual sea surface temperature range of 19–21°C (Bé and Tolderlund 1971; Bé and Gilmer 1977). With exception to this, there is a very short cooler period between 365 and 356cm (Sub-Zone C(ii)) with a higher abundance of *L. retroversa*. During Sub-Zone C (ii) the temperature decreased to between 12–16°C. The surface water then warmed again during Sub-Zone C(i) to between 17–19°C (Bé and Tolderlund 1971; Bé and Gilmer 1977). Cluster analysis shows that there is also some temperature fluctuation during Zone C(i), indicating that samples 240 and 270cm reflect a cold water assemblage (text-fig. 6). In both samples, this is due to increased numbers of *L. retroversa* coinciding with decreased numbers of *H. inflatus* (text-fig. 3). Pteropod species *L. bulimoides* and *C. virgula* return to Zone C with an increase in the abundance of *Diacria trispinosa* (Blainville 1821), a warm water cosmopolitan species of pteropod. The climate switched to reflect a sub-polar assemblage (Zone B) at the MIS 5/4 boundary (71 kyr, 230cm).

Zone B (225–36cm) 71–14 ka

This cool period indicates a major turning point in the climate, with steady cooling throughout MIS 4, 3 and 2, towards the Last Glacial Maximum (MIS 2.2). This is a zone of sub-polar species similar to that of the modern North Atlantic (Bé and Gilmer 1977; Bé 1977). It is characterised by a very high abundance of the sub-polar pteropod *L. retroversa* (up to 100%, with an average of 79% of holoplanktonic gastropods) and the sub-polar planktonic foraminifera *G. bulloides* (average 48% of planktonic foraminifera). There are also higher abundances of the planktonic foraminifera *Globorotalia scitula* (Brady 1882, 10%) and *G. glutinata* (9%), which occupy a range of habitats from sub-polar to equatorial (text-fig. 3). The abundance of the heteropod *A. rosea*, which is only known from warm waters, fluctuates throughout this zone. It is interesting to note that peaks in the occurrence of *A. rosea* occur when the abundance of *L. retroversa* reduces and may therefore signify temperature fluctuations in this sub-polar zone. However, cluster analysis only indicates that one sample (50cm) contains an assemblage comparable to the warm water zones (text-fig. 6). Dominant planktonic foraminifera and pteropod species during this period suggest an annual sea surface temperature range of 7–10°C (Bé and Tolderlund 1971; Bé and Gilmer 1977). This is in agreement with temperature reconstruction data published by Sbaffi et al. (2001) and Hayes et al. (2005).

Zone B is comparable to Zone 3 described by Biekart (1989) in a deep sea core from the Tyrrhenian Sea. Biekart (1989) found similar abundances of *L. retroversa*, but much higher abundances of *D. trispinosa*, which are only present in this section of B5-1 in low numbers (maximum 13%). Chen (1968) also recorded this period of abundant *L. retroversa* in a core collected south of the island of Crete. This zone has also been detected in

**TEXT-FIGURE 7**

Specimens of *Heliconoides inflatus* 1a) and b) from Hole 716B (15–16cm, 150–500µm) have a protruding protoconch; 2a) and b) from B5-1 (0–1cm, >500µm) have a depressed protoconch.

cores throughout the eastern Mediterranean Sea and in the Balearic Sea (Herman 1971), in the Tyrrhenian Sea (Carboni and Esu 1987; Jorissen et al. 1993; Bucceri et al. 2002) and the Adriatic Sea (Jorissen et al. 1993). Capotondi et al. (1999) and Sbaffi et al. (2001) have expanded on the work of Jorissen et al. (1993), splitting the previous 'Zone 3' into more detailed zones. At the top and bottom of Zone B (225cm to 140cm and 50cm to 36cm) an increased abundance of the transitional species *Clio pyramidata* Linnaeus 1767 and *G. inflata* signifies the transition between warm and cold periods. Many authors consider the upper transitional period (50cm to 36cm) as a distinct zone (Carboni and Esu 1989; Jorissen et al. 1993; Bucceri et al. 2002), characterised by an increase in transitional and warmer water species. Capotondi et al. (1999) and Sbaffi et al. (2001) also subdivide this period into smaller bio-zones.

Zone A (35–0cm depth) 14–0 ka

This is a zone of sub-tropical species, which spans MIS 1 (text-fig. 3) and is characterised by a high abundance of the tropical pteropod *H. inflatus* (average 43% of holoplanktonic gastropods) and a very low abundance of the sub-polar pteropod *L. retroversa* (average 1%). The transitional planktonic foraminifera *G. inflata* (13–31% of planktonic foraminifera) and the sub-tropical heteropod *A. selvagensis* (16–21%) also increase in abundance. Zone A contains the warm water pteropods *L. bulimoides* and *C. virgula* and the tropical planktonic

foraminifera *G. siphonifera* and *G. sacculifer* which are not found in Zone B. This assemblage is similar to that found in Holocene sediments described from the Tyrrhenian Sea (Carboni and Esu 1987; Jorissen et al. 1993; Capotondi et al. 1999; Sbaffi et al. 2001; Buccheri et al. 2002), the Adriatic Sea (Jorissen et al. 1993; Capotondi et al. 1999), south of Sicily (Capotondi et al. 1999), in the western Mediterranean Sea (Pérez-Folgado et al. 2003) and south of the island of Crete (Chen 1968). Species present within Zone A indicate a sub-tropical climate similar to that of the modern day western Mediterranean Sea (Bé and Gilmer 1977; Bé 1977). The sea surface temperature at this time, averaged over the entire Mediterranean Sea, ranged from 14–25°C (Sbaffi et al. 2001). At the site of B5-1, dominant planktonic foraminifera and pteropod species suggest an annual sea surface temperature range of 19–21°C (Bé and Tolderlund 1971; Bé and Gilmer 1977).

The Indian Ocean

Due to drilling disturbance at the top of ODP Hole 716B, the uppermost sample at this site was collected at 15–16cm in the core. Assuming the average sedimentation rate of 3.8cmkyr⁻¹ (Backman et al. 1988), this sample likely represents around 4 kyr before the present day. Planktonic species present in the modern overlying waters at ODP Site 716 will, therefore, not be accurately represented within this sample. However, many of the species of holoplanktonic gastropod found within the overlying waters (Tesch 1949; Thiriot-Quiévreux 1973; Bé and Gilmer 1977; Aravindakshan 1977) are also found within the 15–16cm sample. Species missing from the sediments primarily appear to be the larger *Cavolinia* spp. and *Clio* spp. All

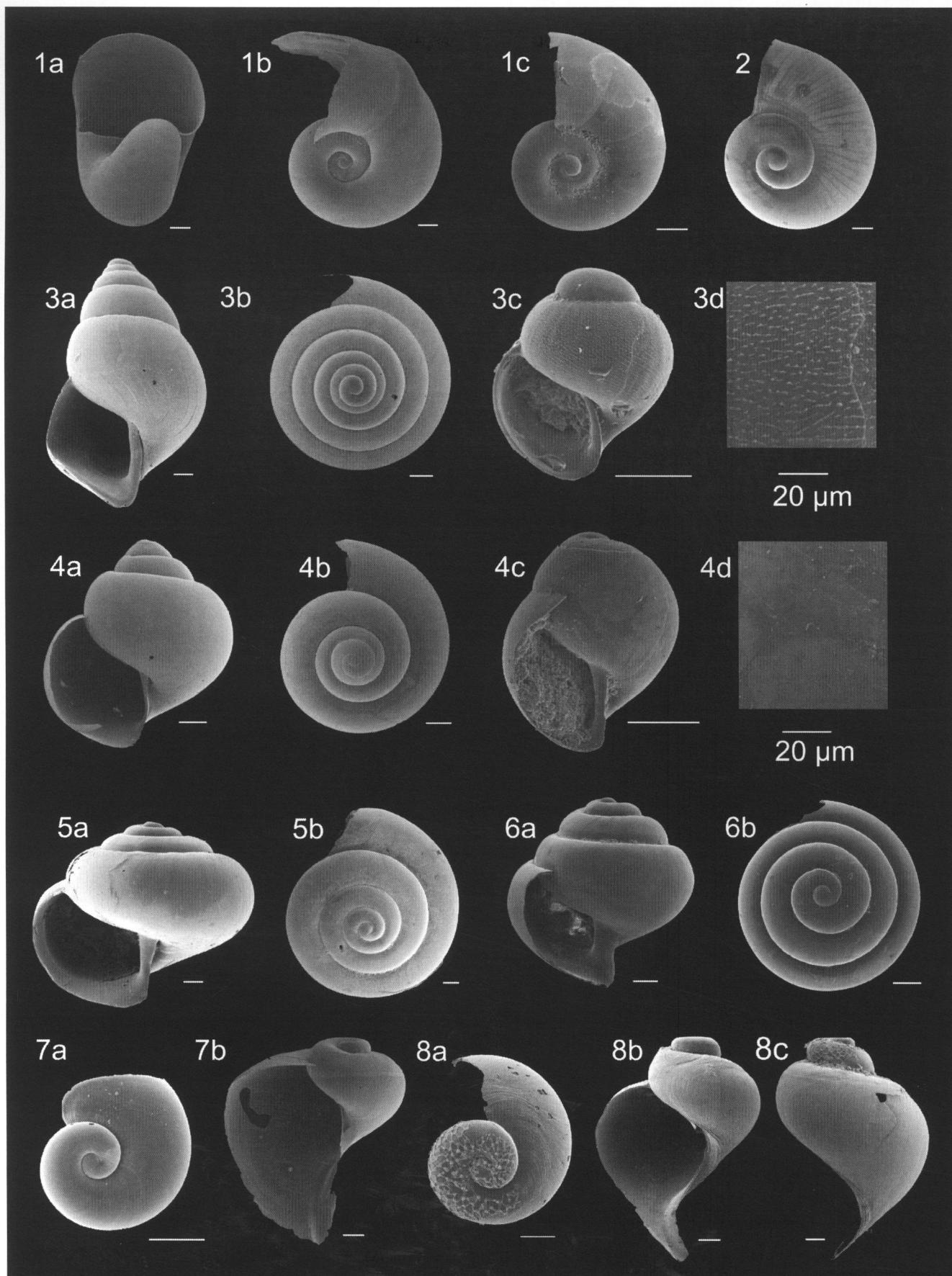
pteropod species found within sample 15–16cm are recorded by Bé and Gilmer (1977) as being present in the overlying waters at ODP Site 716. Fourteen of the twentyone heteropod species recorded as living in the Indian Ocean were found within sample 15–16cm (Tesch 1910; Taki and Okutani 1962; Richter 1974; Aravindakshan 1977; Seapy et al. 2003). The majority of planktonic foraminifera species found in the overlying waters of the Indian Ocean are present within the sample 15–16cm. Species missing from the sample are uncommon in the overlying waters, found only to be ‘present’ (<5%) by Bé and Tolderlund (1971) and Cullen and Prell (1984). These include *Candeina nitida* d’Orbigny 1839 and *H. pelagica*, which are found elsewhere in the core, and *Globigerinoides tenellus* Parker 1958, which was not found in the sediments of ODP Hole 716B. Several species found in the sample 15–16cm of Hole 716B were not recorded from the overlying water. This is both a factor of the 4 kyr gap and also because some species are more recently described, and not recognised by Bé and Tolderlund (1971) or Cullen and Prell (1984). Species found in the sample 15–16cm, but not recorded in the overlying waters include *G. bulloides*, *G. trilobus*, *Globorotalia tumida* (Brady 1877), *Globorotalia theyeri* Fleisher 1974 and *Sphaeroidinella dehiscens* (Parker and Jones 1865).

Similar to the Caribbean Sea, the low latitude location of ODP Hole 716B created a low temperature variation across glacial and interglacial periods of the Late Pleistocene. Consequently, very little change in species composition, species richness (37–46 species) and overall abundance is observed throughout ODP Hole 716B (text-fig. 5). This is supported by the lack of

PLATE 1

Family Limacinidae and Peraclididae. All scale bars represent 100µm, except where stated otherwise.

- 1 *Heliconoides inflatus* a) apertural view (CAR-MON 2, 70cm); b) apical (CAR-MON 2, 70cm); c) apical view (716B, 15cm).
- 2 *Limacina* sp. C a) apical view (CAR-MON 2, 45cm)
- 3 *Limacina bulimoides* a) apertural view (CAR-MON 2, 80cm); b) apical view (CAR-MON 2, 70cm); c) larval shell (B5-1, 20cm); d) larval shell surface (B5-1, 20cm).
- 4 *Limacina trochiformis* a) apertural view (CAR-MON 2, 70cm); b) apical view (CAR-MON 2, 70cm); c) larval shell (B5-1, 0cm); d) larval shell surface (B5-1, 0cm).
- 5 *Limacina lesueurii* a) apertural view (CAR-MON 2, 30cm); b) apical view (CAR-MON 2, 30cm).
- 6 *Limacina retroversa* a) apertural view (B5-1, 210cm); b) apical view (B5-1, 210cm).
- 7 *Peracle moluccensis* a) larval shell (CAR-MON 2, 365cm); b) apertural view (CAR-MON 2, 360cm).
- 8 *Peracle diversa* a) apical view (CAR-MON 2, 350cm); b) apertural view (CAR-MON 2, 70cm); c) side view (CAR-MON 2, 75cm).



significant synchronous changes between oxygen isotope data and the relative abundances of temperature sensitive species (text-fig. 5). Barrows and Juggins (2005) reconstruct the sea-surface temperature at ODP Site 716 to range between 25–28°C at the Last Glacial Maximum (18cm core depth, MIS 2.2). The mean annual sea-surface temperature close to ODP Site 716 at this time was 27°C, just one degree lower than that of today (Barrows and Juggins 2005). Cullen and Droxler (1990) reconstruct the sea surface temperature at ODP Site 716 to be below 26°C during MIS 6–8 and suggest that any variation in species abundances are more likely to be due to changes in other environmental parameters, such as salinity and nutrient availability. The species assemblage throughout ODP Hole 716B is composed of warm water sub-tropical species of planktonic foraminifera, pteropods and heteropods, with some transitional species. The dominant planktonic foraminifera species is *Globorotalia menardii* (d'Orbigny 1826), making up to 39% of planktonic foraminifera. Other abundant species include *G. sacculifer* (including *G. trilobus*), *N. dutertrei* and *Globogaudrya quadrina conglobata* (Schwager 1866). *G. siphonifera* and *O. universa* are also common throughout the core. The pteropod genera *Limacina* and *Helioconoides* dominate the assemblage of holoplanktonic gastropods, the most abundant species being *H. inflatus* (up to 66% of the holoplanktonic gastropod population of Hole 716B). Other common and often abundant species of pteropod include *L. trochiformis* and *Clio convexa* (Boas 1886). The dominant heteropod genus is *Atlanta*, with common and often abundant heteropod species including *A. frontieri* and *C. lamarckii*.

DISCUSSION

The application of holoplanktonic gastropods in stratigraphy

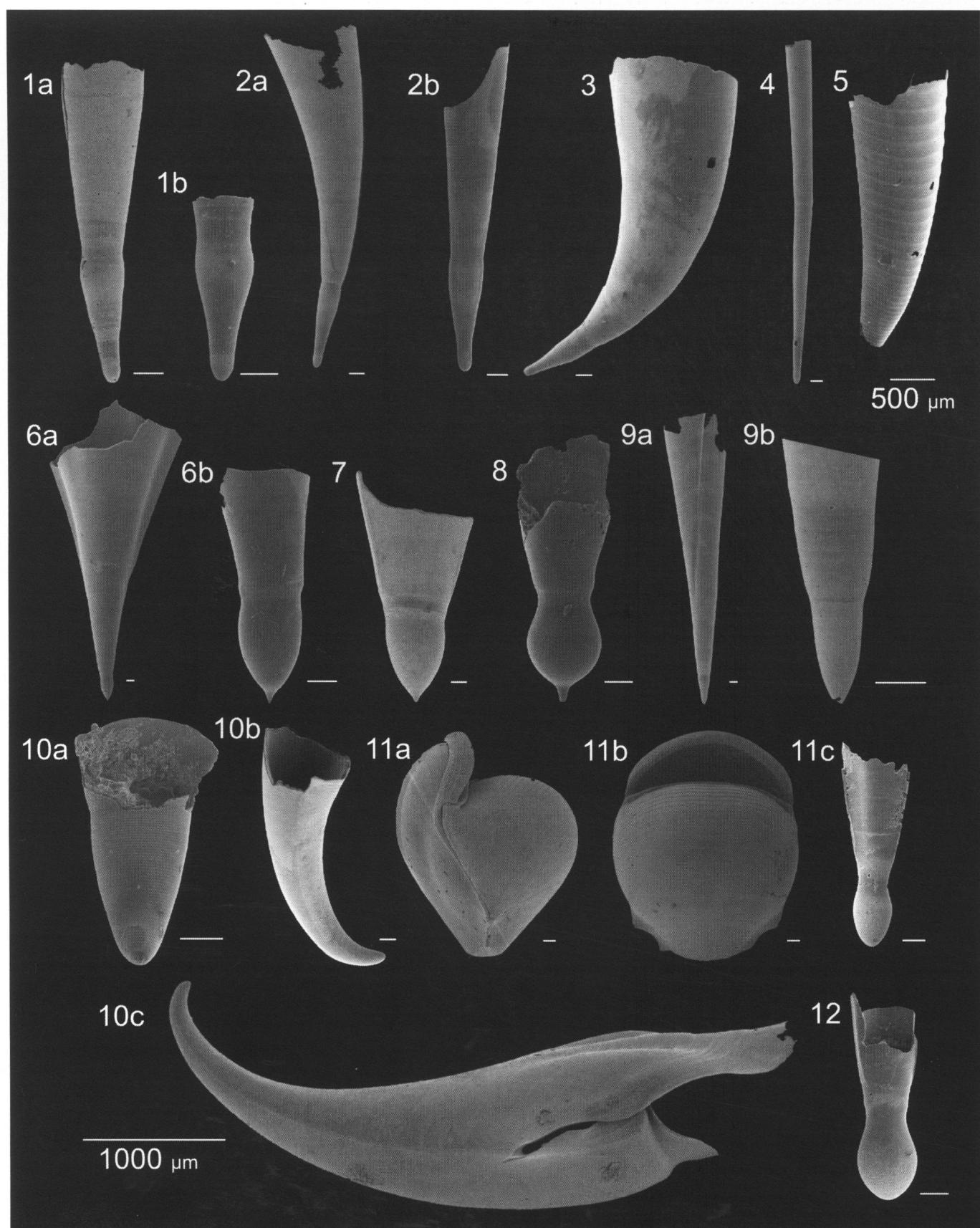
The results of this study demonstrate that the success of using down-core distributions of holoplanktonic gastropods as biostratigraphical markers is variable. Changes in temperature appear to drive changes in the assemblage composition, therefore, identifying MIS boundaries using species assemblages is only possible where water temperature changes considerably through time. This method proved useful in the Mediterranean Sea, where amplification of the climatic changes lead to substantial changes in holoplanktonic gastropod assemblage. However, in low latitude locations, such as the Caribbean Sea and Indian Ocean, where temperature changes are less significant, variations in species composition were not evident and could not be used to identify the positions of MIS. This is, however, also true for the assemblages of planktonic foraminifera, which are more widely used in biostratigraphy. In this study, no first or last occurrences of species were identified. Further research upon a longer record of holoplanktonic gastropods is necessary to identify these datum species, which would undoubtedly enhance their use in biostratigraphy.

Despite the variable success of using holoplanktonic gastropods for biostratigraphy, this study demonstrates their consistent use as a tool in reconstructing paleoenvironments. In particular, temperature ranges for the Mediterranean Sea were constrained by using the known temperature ranges of pteropod species combined with ranges for planktonic foraminifera. Further research into the environmental requirements of living holoplank-

PLATE 2

Family Cavoliniidae. All scale bars represent 100µm, except where stated otherwise.

- 1 *Creseis chierchiae* a) adult shell (716B, 15cm); b) protoconch (716B, 15cm).
- 2 *Creseis virgula* a) adult shell (CAR-MON 2, 70cm); b) protoconch B5-1, 20cm).
- 3 *Creseis virgula* adult shell (CAR-MON 2, 30cm).
- 4 *Creseis clava* adult shell (CAR-MON 2, 70cm).
- 5 *Hyalocylis striata* (CAR-MON 2, 80cm).
- 6 *Clio pyramidata* a) adult shell (CAR-MON 2, 80cm); b) protoconch (B5-1, 90cm).
- 7 *Clio convexa* protoconch (716B, 15cm).
- 8 *Clio cuspidata* protoconch (B5-1, 20cm).
- 9 *Styliola subula* a) adult shell (CAR-MON 2, 80cm); protoconch (CAR-MON 2, 80cm).
- 10 *Cavolinia inflexa* a) protoconch (B5-1, 20cm); b) protoconch (CAR-MON 2, 80cm); c) adult shell (CAR-MON 2, 80cm).
- 11 *Diacria quadridentata* a) adult shell, side view (CAR-MON 2, 70cm); b) apertural view (CAR-MON 2, 70cm); c) protoconch (CAR-MON 2, 20cm).
- 12 *Diacria trispinosa* protoconch (CAR-MON 2, 0cm).



tonic gastropods will increase their use in paleoenvironmental interpretations.

Previously undescribed species

Down-core distributions have revealed three species of holoplanktonic gastropod that are potentially previously undescribed, or that were previously assumed to be extinct. A number of specimens of the heteropod '*Atlanta* sp. D' (Plate 3, figs. 3 a–c) were found in Caribbean Sea sediments. This species appears to be previously undescribed and may, therefore, represent a new species. Further to this, pteropod specimens, thought to be *Heliconoides mermuysi*, but potentially larval shells of the benthic gastropod Architectonicidae, were found in sediments from the Caribbean Sea and Indian Ocean. The descriptions of these species can be found below. During microfossil analysis, it was also noticed that some specimens of *H. inflatus* from ODP Hole 716B showed a slightly different morphology from specimens collected in both the Caribbean Sea and the Mediterranean Sea. Although adult forms remain an overall depressed shape, the protoconch and first whorl of Indian Ocean specimens were found to be slightly raised in comparison to specimens from other locations (text-fig. 7). Although this is only a slight variation of the morphology, it may indicate a new sub-species of *H. inflatus* and requires further investigation.

Limacina sp. C [*Heliconoides mermuysi*?]

Plate 3, figure 1 a–c

Diagnosis: A shell similar in size and morphology to *H. inflatus* but with whorls that inflate more gradually. The aperture is circular and the apertural margin ends in a thickened rim. The apex protrudes slightly.

Remarks: The morphology of *Limacina* sp. C is very similar to species belonging to the genus *Heliconoides*, in particular *H. mermuysi* as described by Cahuzac and Janssen (2010) exclusively from Moulin de Cabanes. However, the morphology is also similar to larval shells of the Architectonicidae. The specimens are all in good condition and are unlikely to be the result of sediment reworking. Fifteen specimens were collected in total from the >500 µm fraction throughout CAR-MON 2 and from the >500 µm and 150–500 µm of Hole 716B. The youngest specimen was collected at 10 cm core depth in CAR-MON 2, which is approximately 4 kyr.

Distribution: During this study, *Limacina* sp. C was found in the Caribbean Sea and in the Indian Ocean and showed no temperature preference through the cores.

Atlanta sp. D

Plate 4, figure 11a–b

Diagnosis: A relatively large, highly spired, conical shell, with up to four whorls. The whorls are flat-topped at the sutures, giving a step shape in side-on profile. The umbilicus is large and open.

Remarks: This species is similar in form to *Atlanta inclinata* but has flat-topped whorls. Specimens found are assumed to be juvenile forms as no specimens with a large final whorl, typical of the Atlantidae, were found. Thirteen specimens were collected from the 150–500 µm fraction and six from the >500 µm fraction of CAR-MON 2. The most recent specimen was found at 40 cm core depth, which equates to around 17 kyr.

Distribution: *Atlanta* sp. D was only found in the Caribbean Sea during this study. This species appears to have a preference for warm climates, all specimens except three (150–500 µm: 570 and 575 cm; >500 µm: 60 cm) were found during interglacial periods.

Extended geographical range of heteropods

Down-core distributions of heteropods suggest that their environmental requirements are much broader than previously thought. All species of heteropods in the modern oceans are assumed to be restricted to sub-tropical warm waters (Thiriott-Quiévreux 1973; Van der Spoel 1976). However, this study shows that, during cold, glacial periods in the Mediterranean Sea, up to 29% of the holoplanktonic gastropod assemblage was made up of heteropods. This indicates that extant species of heteropod are able to live in cold sub-polar water. This finding has implications for future research, particularly regarding ocean acidification in the modern oceans, which is predicted to affect aragonitic shelled gastropods in polar and sub-polar waters as soon as 2016 (Steinacher et al. 2009).

Results also highlight the importance of heteropods to the ocean food web. Heteropods are not well studied and poor sampling techniques have led to an underestimation of their numbers in our oceans. Heteropods have large eyes and the ability to swim (Lalli and Gilmer 1989), which allows them to avoid collection in plankton nets (Seapy 1990). The results of this study show that heteropod shells often make up a large proportion of the holoplanktonic gastropod assemblage of sediments (up to 32% in the Caribbean Sea and Indian Ocean and up to 69% in the Mediterranean Sea), which suggests that they are an important component of the ocean food web.

CONCLUSIONS

The results of this study provide new information on the distribution, taxonomy and ecology of holoplanktonic gastropods and planktonic foraminifera through the Late Pleistocene. In all cores analysed, comparison of core top sediments to modern-day overlying waters, suggests that microfossils present within the sediments are representative of the species richness and relative abundances of the overlying waters at the time of deposition. These data provide the first information on both fossil and modern heteropods in the Caribbean Sea, as well as providing an extended and enhanced distribution of holoplanktonic gastropods and planktonic foraminifera in the Mediterranean Sea and Indian Ocean. The success of using holoplanktonic gastropods in biostratigraphy was found to be variable and generally only of use in locations that had experienced considerable changes in temperature over time. However, their application to paleoenvironmental reconstructions was found to be consistently valuable, often improving upon the use of planktonic foraminifera to calculate a range of temperature. More research into the first and last occurrences of a long holoplanktonic gastropod record would greatly improve their use in biostratigraphy.

The revelation that heteropods have a wider geographical range and make up a larger proportion of the ocean food web, as well as the discovery of potential new species and a pteropod species only recognised from the Miocene, highlights the surprisingly poor understanding that we still have of holoplanktonic gastropod ecology and taxonomy. Much further research is required in this field and would be timely, since the threat from climate change and ocean acidification in the modern oceans, means

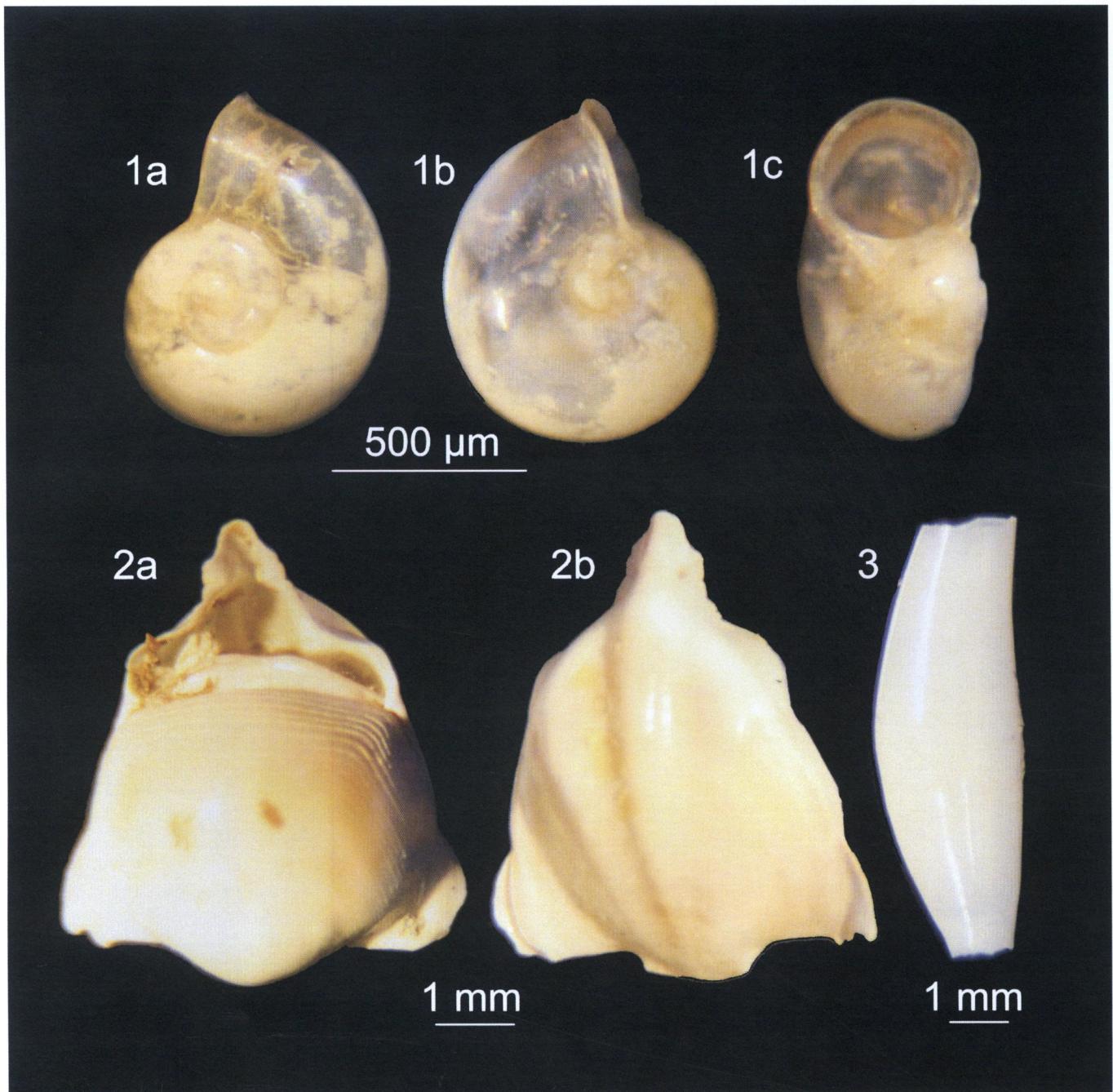


PLATE 3
Family Limacinidae and Cavoliniidae photomicroscope images

- 1 *Limacina* sp. C (CAR-MON 2, 50cm): a) apical view; b) umbilical view; c) apertural view.
- 2 *Diacavolinia longirostris* (CAR-MON 2, 5cm): a) ventral and apertural view; b) dorsal view.
- 3 *Cuvierina columnella* (CAR-MON 2, 310cm) side view.

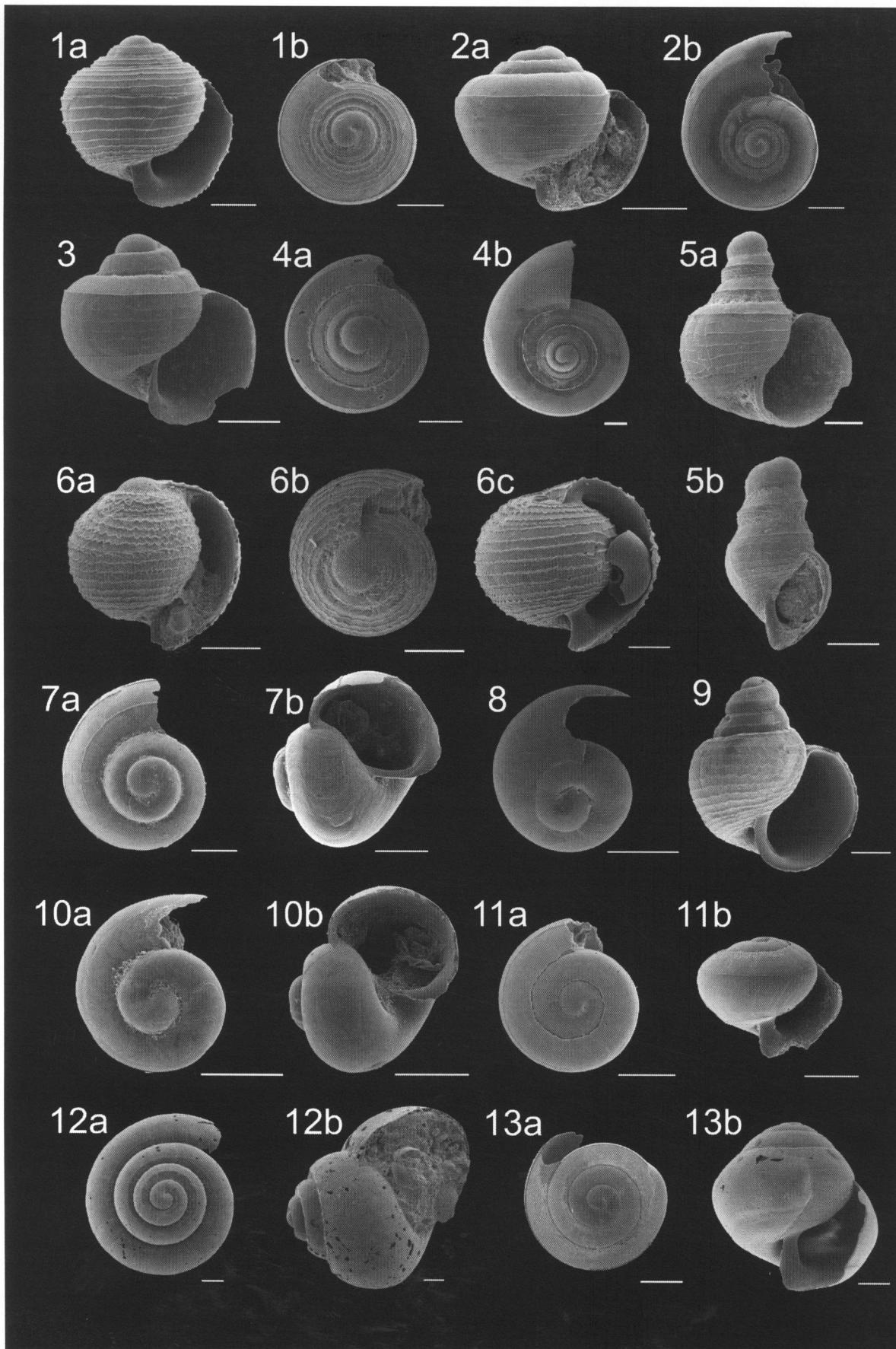
that some species may become extinct before they have even been fully 'discovered'.

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- PLATE 4**
Family Atlantidae juvenile forms. All scale bars represent 100 μm .
- 1 *Atlanta helicinaoidea* a) apertural view (CAR-MON 2, 520cm); b) apical view (716B, 855cm).
- 2 *Atlanta selvagensis* a) apertural view (716B, 75cm); b) apical view (B5-1, 290cm).
- 3 *Atlanta plana* apertural view (716B, 855cm).
- 4 *Atlanta frontieri* a) apical view (716B, 775cm); b) apical view (716B, 475cm).
- 5 *Atlanta turriculata* a) apertural view (716B, 75cm); b) apertural view (716B, 75cm).
- 6 *Oxygyrus inflatus* a) apertural view (716B, 75cm); b) apical view (716B, 75cm); c) apertural view (CAR-MON 2, 90cm).
- 7 *Protatlanta souleyeti* a) apical view (716B, 75cm); b) apertural view (716B, 75cm).
- 8 *Atlanta rosea?* apical view (B5-1, 150cm).
- 9 *Atlanta brunnea* apertural view (CAR-MON 2, 350cm).
- 10 *Atlanta peronii?* a) apical view (CAR-MON 2, 90cm); b) apertural view (B5-1, 20cm).
- 11 *Atlanta tokioka?* a) apical view (716B, 855cm); b) apertural view (716B, 855cm).
- 12 *Atlanta* sp. D a) apical view (CAR-MON 2, 80cm); b) apertural view (CAR-MON 2, 40cm).
- 13 *Atlanta tokioka* a) apical view (CAR-MON 2, 520cm); b) apertural view (CAR-MON 2, 520cm).

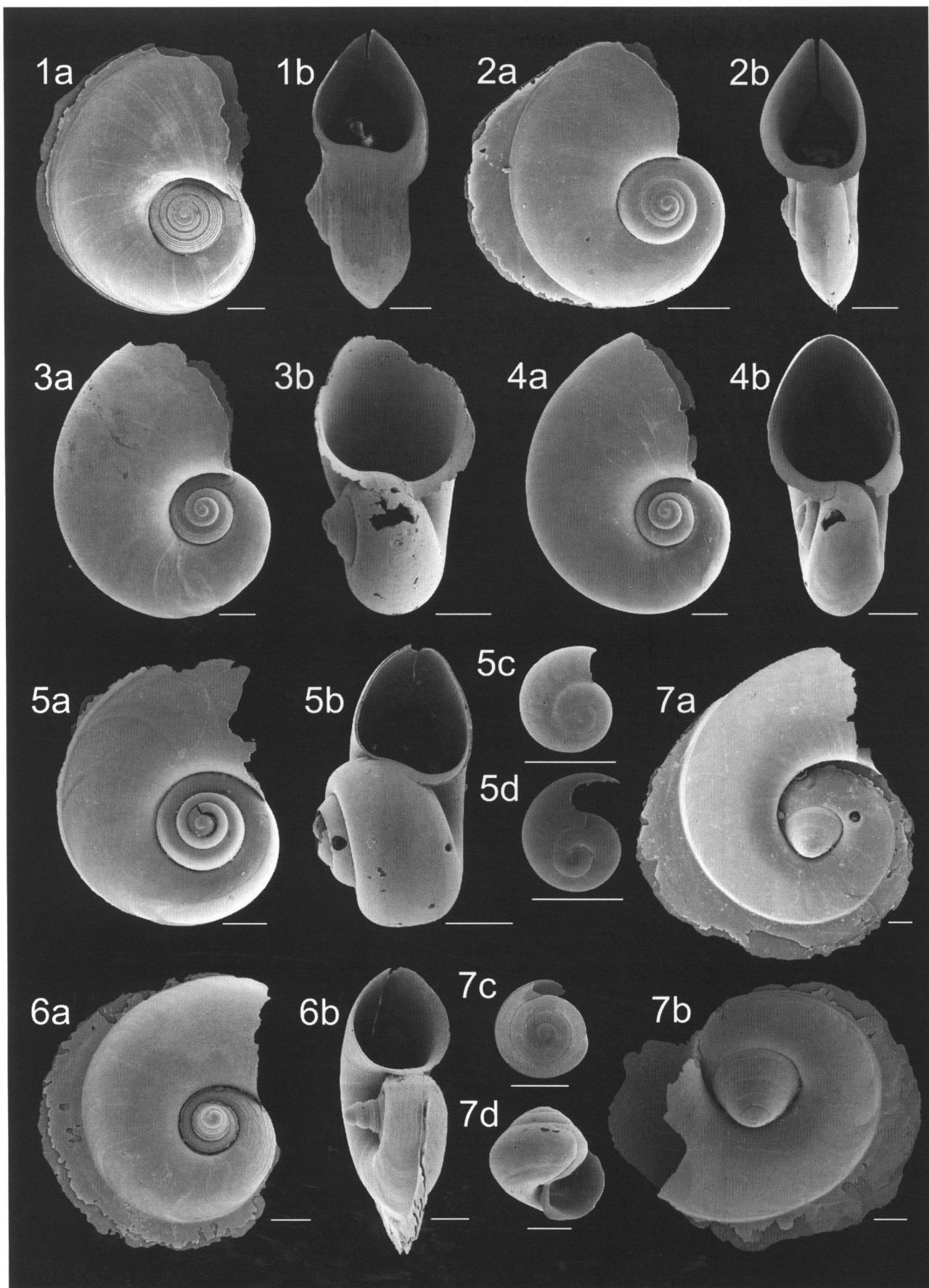


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PLATE 5

Family Atlantidae adult forms. All scale bars represent 200µm.

- 1 *Atlanta helicinaoidea* a) apical view (CAR-MON 2, 75cm); b) apertural view (CAR-MON 2, 75cm).
- 2 *Atlanta selvagensis* a) apical view (CAR-MON 2, 75cm); b) apertural view (CAR-MON 2, 75cm).
- 3 *Protatlanta souleyeti* a) apical view (CAR-MON 2, cm); b) apertural view (CAR-MON 2, cm).
- 4 *Protatlanta souleyeti* a) apical view (CAR-MON 2, 75cm); b) apertural view (CAR-MON 2, 75cm).
- 5 *Atlanta rosea?* a) apical view (CAR-MON 2, 70cm); b) apertural view (CAR-MON 2, 75cm); c) juvenile (B5-1, 150cm); d) juvenile (B5-1, 150cm).
- 6 *Atlanta turriculata* a) apical view (CAR-MON 2, 80cm); b) apertural view (CAR-MON 2, 80cm).
- 7 *Atlanta tokioka?* a) large specimen apical view (CAR-MON 2, 80cm); b) apical view (CAR-MON 2, 80cm); c) juvenile apical view (CAR-MON 2, 520cm); d) juvenile apertural view (CAR-MON 2, 520cm).



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PLATE 6
Family Carinariidae, Clionidae and Cymbuliidae. All scale bars represent 100 μ m.

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|---|--|---|---|
| 1 | <i>Carinaria lamarckii</i> a) larval shell apical view (B5-1, 370cm); b) umbilical view (B5-1, 370cm). | 5 | <i>Firoloida desmarestia</i> a) adult shell apertural view (B5-1, 30cm); b) apical view (B5-1, 30cm); c) juvenile shell (B5-1, 10cm). |
| 2 | <i>Carinaria</i> sp. larval shell (B5-1, 310cm). | 6 | <i>Gleba cordata</i> a) and b) larval shell (B5-1, 240cm). |
| 3 | <i>Carinaria</i> sp. (<i>galea?</i>) larval shell (B5-1, 50cm). | 7 | <i>Gymnosome veliger</i> (B5-1, 440cm). |
| 4 | <i>Carinaria pseudorugosa</i> a) apical view (B5-1, 20cm); b) apertural view (B5-1, 20cm). | 8 | <i>Paedoclione doliformis</i> larval shell (B5-1, 90cm). |

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